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Ecological Genetics of *Pinus contorta* in the Lower Snake River Basin of Central Idaho

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RESEARCH SUMMARY

Genetic differentiation of 89 populations of *Pinus contorta* primarily from central Idaho was assessed by a series of three studies involving (1) growth and development in field environments, (2) the periodicity of shoot elongation in the greenhouse, and (3) freezing tolerance in the laboratory. Population differentiation was detected for a variety of traits that included 3-year height, leaf length, freezing tolerance, and the pattern of shoot elongation. Regression models related as much as 77 percent of the variance among population means to the elevation and geographic location of the seed origin. Elevational clines were steep but geographic clines were gentle. Consequently, if maladaptation is to be controlled in artificial reforestation, seed transfer should be restricted severely for elevation but may be relatively liberal geographically. Detailed practical guidelines for regulating seed movement will be presented separately.

Ecological Genetics of *Pinus contorta* in the Lower Snake River Basin of Central Idaho

G. E. Rehfeldt

INTRODUCTION

Adaptation of populations to the physical environment is the subject of a series of studies on the ecological genetics of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) from the Rocky Mountains. The present study of populations from central Idaho is intended to (1) assess adaptive differentiation among populations and (2) relate patterns of genetic variation to geography, topography, physiography, and climate.

Adaptive differentiation of lodgepole pine populations in both the United States (Rehfeldt 1985b; Stoneman 1985; Hoff 1985) and Canada (Lindgren and others 1980; Hagner 1980; Ying and others 1985) parallels environmental gradients. Consequently, clines in the rugged Rocky Mountains of the United States tend to be steep, while those for regions of dissected plateaus in British Columbia tend to be gentle. Regardless of whether geographic clines predominate, as in British Columbia (Ying and others 1985), or whether altitudinal clines predominate, as in the Rocky Mountains of the United States (Rehfeldt 1985b), populations from relatively mild environments display a high growth potential and low cold hardiness, while populations from severe environments exhibit a low growth potential and high hardiness.

Consequently, seed transfer for reforestation in northern Idaho (Rehfeldt 1983), Utah (Rehfeldt 1985a), and central Oregon (Stoneman 1985) must be restricted greatly if maladaptation and resultant losses in productivity are to be controlled. Practical application of the present study involves developing seed transfer guidelines for lodgepole pine in central Idaho.

MATERIALS AND METHODS

Population differentiation was studied in seedlings from 89 populations. Of these populations, 80 represented the geographic distribution and ecologic amplitude of the species in the lower Snake River Basin in central Idaho. Eight populations were from the Cascade Mountains of south-central Oregon, and one represented a small disjunct population from Deadline Ridge in southern Idaho (fig. 1). Seedlings from the 89 populations were used in separate studies of: (1) growth and development in field environments, (2) periodicity of shoot elongation in a greenhouse, and (3) cold hardiness in the laboratory. Because cone collections, experimental

procedures, and statistical analyses are detailed in the first paper of this series, which involved populations from the Wasatch and Uinta Mountains of Utah (Rehfeldt 1985a), only an outline follows.

Growth and Development

One set of seedlings from each of the 89 populations was grown for 6 months in plastic containers (10 in³) in a shadehouse at Moscow, ID (lat. 48.5° N., long. 116.7° W.). In the fall, seedlings were transplanted into two environments, 2,200 feet and 5,000 feet elevation, at

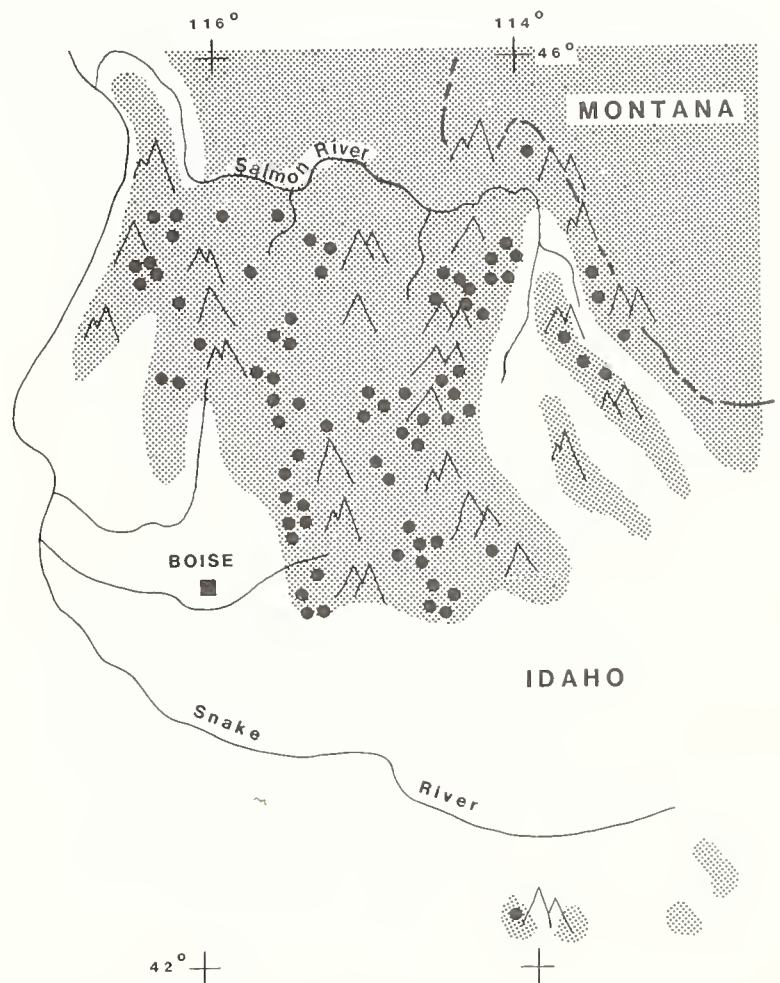


Figure 1.—Geographic distribution of *Pinus contorta* (shading, according to Little 1971) within the region of study and location of populations (symbols).

the Priest River Experimental Forest, 150 miles north of Moscow. Eight seedlings spaced at 1 foot and 0.5 foot at low and high elevation sites, respectively, were planted in row plots, separated by 1.5 feet and 1 foot at the respective sites. Three blocks were established at each site, and both plantings were maintained under intensive management.

The performance of individual seedlings was described by four variables for which differentiation of Utah populations had been pronounced: (1) height—seedling height after 3 years; (2) late growth—amount of the 3-year predetermined shoot that elongated after the fourth week of elongation in the respective environments; (3) leaf length—the length of a leaf near the center of the 3-year shoot; and (4) adjusted height—3-year height adjusted by regression on 2-year height. By representing the increment from a common 2-year height, adjusted height is relatively independent of previous environmental (such as transplanting shock) and genetic effects and thereby is capable of reflecting adaptation of populations to a particular environment for a single growing season.

In addition, scores were made of the presence or absence of injury from a freeze (16 °F) that occurred in mid-May at the low elevation site. Injuries ranged from death of the developing shoot to reductions in internode lengths near the shoot tip.

To account for heterogeneous variances at the two test environments, data were transformed to standard normal deviates (Steel and Torrie 1960) for each test site and the deviates were analyzed according to a model of random effects. The model estimated: (1) main effects for test environments, blocks within environments, and populations; (2) the interaction of populations $\times$ environments; (3) an experimental error, composed of the interaction of populations $\times$ blocks within environments; and (4) a residual error. As a result of the transformations, mean squares associated with the main effects of test environments were zero. A harmonic mean of 7.20 reflected the number of seedlings represented in each block.

Injury from the spring frost was analyzed according to a model of random effects, which estimated effects of blocks, populations, and an error.

Periodicity of Shoot Elongation

Another set of seedlings grew for 1 year in plastic containers (45 in³) in a shadehouse at Moscow. Each population was represented by nine seedlings in each of three blocks. In early March of the second growing season, seedlings were moved into a greenhouse before shoot elongation had begun. Greenhouses were maintained under natural lighting. Temperatures were about 75 °F during the day and 55 °F at night. All seedlings were measured three times each week until elongation of the preformed bud had ceased.

As described by Rehfeldt and Wykoff (1981), shoot elongation of individual trees was expressed mathematically by a logistic function that included a hyperbolic time term. Regression statistics allowed calculation of the following variables for describing periodicity of shoot

elongation of individual seedlings: (1) initiation of growth—the day on which 0.1 inch of cumulative growth had occurred; (2) cessation of growth—the day on which all but 0.1 inch of growth had occurred; (3) duration of growth—the number of days between initiation and cessation; (4) rate of growth—elongation per day during the period of maximum elongation; and (5) total elongation.

Population differentiation was assessed according to least squares analyses of random effects that estimated main effects for populations and blocks, the interaction of populations $\times$ blocks, and an error. A harmonic mean of 8.81 reflected the number of seedlings representing each population in each block.

Cold Hardiness

To estimate the relative cold hardiness of populations in early autumn, laboratory tests of freezing tolerance were made according to the general procedures of Levitt (1972). Mature leaves were collected in late September from near the center of the 3-year shoot of trees represented in field tests at 5,000 feet elevation.

Four sets of eight leaves were collected from each eight-tree plot. Each set contained one leaf from each tree. One set of leaves from each plot was exposed to one of four test temperatures (−4 °F, −6 °F, −10 °F, and −12 °F) by cooling at the rate of 10 °F/h. Injured leaves were identified visually by the presence of discolored and flaccid tissue (Rehfeldt 1980). Population differentiation for the proportion of injured leaves from each plot was assessed from a model of random effects that allowed estimation of main effects for populations, blocks, and test temperatures; three two-way interactions; and a residual.

Patterns of Variation

Geographic patterns of genetic variation were assessed from a series of regression analyses that fitted independent variables describing the origin of populations to the array of population means. Because the primary purpose of these analyses was to describe genetic patterns of variation for the lower Snake River Basin, regression analyses considered only the 80 representative populations. The sequence of regression analyses concentrated first on the relationship between performance and elevation of the seed source, and second on geographic patterns of variation that were independent of elevation. Adequacy of a model was judged according to the goodness of fit (R^2), residual variance ($s_{y,x}$), and geographic or ecologic patterns displayed by residuals (Draper and Smith 1966).

Elevational models considered both a linear and quadratic relationship between performance and elevation of the seed source. Deviations from the best fitting elevational regressions were then used as dependent variables for considering geographic patterns of variation that were independent of elevation. The geographic model included four independent variables plus their squares: latitude, longitude, northwest departure, and northeast departure. The latter two variables were obtained by rotating the grid of latitude and longitude by 45°. Thus, eight independent variables were included in the model.

which was fitted with a stepwise regression program for maximizing R^2 (Barr and others 1979). Finally, elevation of the seed source was added to the independent variables of the best fitting geographic model in order to estimate the joint determination of performance by geography and elevation for those variables in which previous models had been significant.

RESULTS

Because each study was autonomous, the results of each are presented separately but are considered jointly in establishing patterns of genetic variation.

Growth and Development

The effects of planting environment on growth and development of seedlings were pronounced for all traits (table 1). Trees growing at low elevation were much taller and had longer leaves than those at high elevation. Adjusted heights show that even if all trees had been the same height at age 2, those growing at low elevation would still have been tallest after 3 years. Late growth, defined as the proportion of the predetermined shoot that elongated after the fourth week, was measured at the low elevation approximately 5 weeks earlier than at the high, and therefore also was affected tremendously by the environment.

For nearly all variables, the range in population mean values was considerably different at the two planting environments (table 1). For these ranges to differ greatly illustrates the heterogeneous variances that required adjustment before statistical analyses were made.

By accounting for over a third of the total variance, effects of populations were pronounced for 3-year height and frost injury (table 2). These strong effects are illustrated by mean differences between populations of as much as 1 foot in height and 58 percent in trees injured by frost. On the average, trees damaged by frost were 2.5 inches shorter after 3 years than uninjured trees from the same population. Relatively weak effects for late growth contrast sharply with previous results (Rehfeldt 1985a) and likely are due to the late stage of elongation at which current measurements were begun: the average tree produced only 12 percent of the 3-year shoot as late growth. Consequently, mean values for populations ranged from only 0.6 inch to 1.4 inches. Populations also differed by as much as 0.8 inch in leaf length. But no differences could be detected among populations for adjusted height, a result that is partially influenced by the significant regression of 3-year height on 2-year height, which accounted for 70 percent of the variance in 3-year height of individual trees.

Significant interactions of populations and environments were apparent for leaf length and adjusted height. The interaction for leaf length is best interpreted as sampling errors associated with slightly different estimates of mean values for a given population at the two planting sites. But the interaction for adjusted height developed from divergent performance of individual populations in the two environments. This interaction will be considered later when patterns of variation for mean values of this trait are considered from both test sites. The size of this interaction, however, explains the lack of main effects of populations for adjusted height.

Table 1.—Mean values according to test environment and range of population means in each environment

Variable		Mean values at		Range in population means at	
		2,200 ft	5,000 ft	2,200 ft	5,000 ft
Late growth	(inches)	1.2	0.6	1.3	0.4
Leaf length	(inches)	2.8	2.4	0.9	1.1
Height	(inches)	16.6	13.4	15.5	7.4
Adjusted height	(inches)	16.0	14.0	6.8	3.1
Frost injury	(percent)	15	—	58	—

Table 2.—Results of analyses of variance for growth and development presented as intraclass correlations, the ratio of individual variance components to the sum of all components

Source of variance	Variable				
	Late growth	Leaf length	Height	Adjusted height	Frost injury
Environments	0	0	0	0	0
Blocks in environment	0.04**	0.04**	0.03**	0.01*	0.01*
Populations	.05**	.07**	.41**	— .01	.33**
Environment × population	0	.05**	.02**	.31**	—
Experimental error	.11**	.08**	.05**	.04**	—
Within plots	.80	.76	.49	.72	.67

*Statistical significance of the F-value at the 5 percent level of probability.

**Statistical significance of the F-value at the 1 percent level of probability.

Periodicity of Shoot Elongation

The logistic function described periodicity of shoot elongation of individual trees nearly perfectly. Values of R^2 ranged from 0.93 to essentially 1 while averaging 0.99. Analyses of variance detected significant differences (fig. 2) among populations for all variables but were particularly strong for the duration, cessation, and amount of shoot elongation (table 3). For these variables, main effects of populations accounted for more than 30 percent of the total variance. Differences between populations were as large as 18 days in cessation, 17 days in duration, 2 days in initiation, 0.1 inch per day in rate, and 3.2 inches in the amount of elongation. Most of the differences among populations in the initiation of shoot elongation resulted from delayed initiation of sources from the Cascade Mountains. Differences among populations from central Idaho amounted to only 1 day.

Cold Hardiness

Effects of test temperatures dominated analyses of variance (table 4). These effects are associated with a range in injury from 27 percent at -4°F to 70 percent at -12°F . Effects of populations were significant and accounted for 12 percent of the total variance. Mean differences among populations amounted to as much as 70 percent injured leaves.

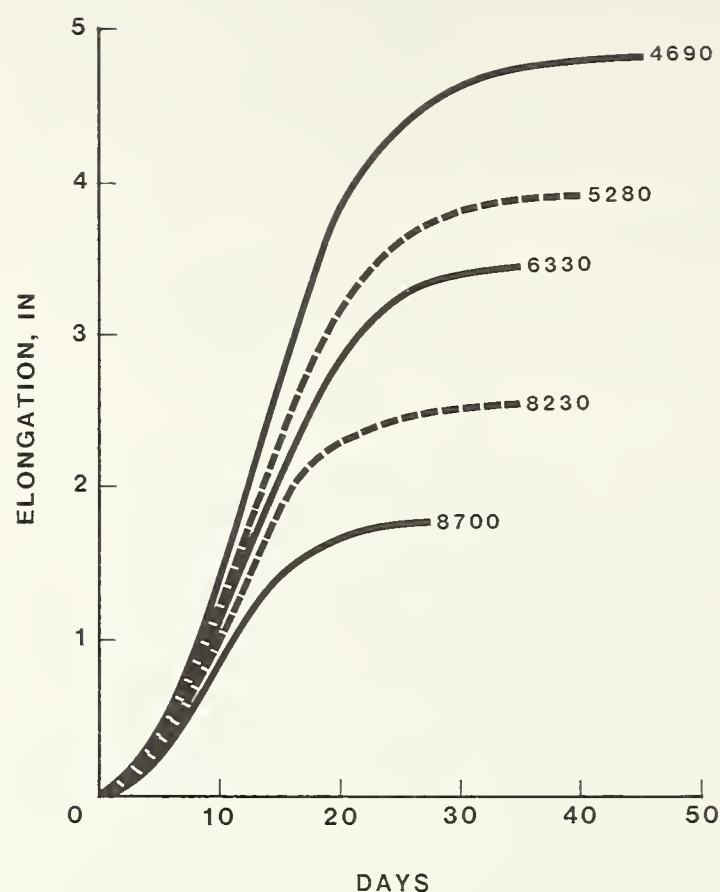


Figure 2.—Periodicity of shoot elongation for populations from a range of elevations (feet) that represented maximum differences in response.

Table 3.—Results of analyses of variance for periodicity of shoot elongation presented as intraclass correlations, the ratio of a variance component to the sum of all components

Source of variance	Initiation	Duration	Rate	Cessation	Elongation
Blocks	0.01*	0.01*	0.02*	0.01*	0.02*
Populations	.12*	.29*	.14*	.30*	.37*
Interaction	.10*	.04*	.17*	.03*	.12*
Within plots	.77	.73	.67	.66	.49

*Statistical significance of the F-value at the 1 percent level.

Table 4.—Results of analyses of variance of freezing tests presented as intraclass correlations, the ratio of a variance component to the sum of all components

Source of variance	Intraclass correlation
Blocks	0.01*
Temperatures	.23**
Populations	.12**
Populations $\times$ temperatures	0
Residual ¹	.64

*Statistical significance of the F-value at the 5 percent level.

**Statistical significance of the F-value at the 1 percent level.

¹Composed of the two interactions involving populations.

Patterns of Variation

Elevation of the seed source had a pronounced effect on performance of populations. Elevational models accounted for more than 60 percent of the variance between populations for four variables and were statistically significant for all variables except the initiation of shoot elongation (table 5 and fig. 3). As elevation of the

seed source increased, growth potential decreased, largely because of an associated decline in late growth and in the rate, duration, and cessation of shoot elongation. Leaf lengths also declined with increasing elevation, but freezing tolerance increased. Quadratic models provided a significant reduction in the residual mean square of the linear model for only late growth, leaf length, and adjusted height at 2,200 feet.

Table 5.—Coefficients of determination (R^2) for regression analyses relating genetic variation to geographic and physiographic variables

Variable	Elevational models		Geographic model	Combined model
	Linear	Quadratic		
Growth and development				
Late growth	0.17**	0.21**	0	—
Leaf length	.36**	.39**	0.12**	0.52**
Height	.69**	.69**	.14**	.74**
Adjusted height (2,200 ft)	.42**	.47**	.23**	.60**
Adjusted height (5,000 ft)	.21**	.21**	.09*	.28**
Frost injury	.42**	.42**	.18**	.54**
Periodicity of shoot elongation				
Initiation	0	.01	0	—
Duration	.64**	.64**	.21**	.71**
Rate	.48**	.50**	.07*	.52**
Cessation	.64**	.64**	.22**	.72**
Elongation	.66**	.67**	.23**	.73**
Cold hardiness				
Injury	.42**	.42**	.08	—

*Statistical significance at the 5 percent level of probability.

**Statistical significance at the 1 percent level of probability.

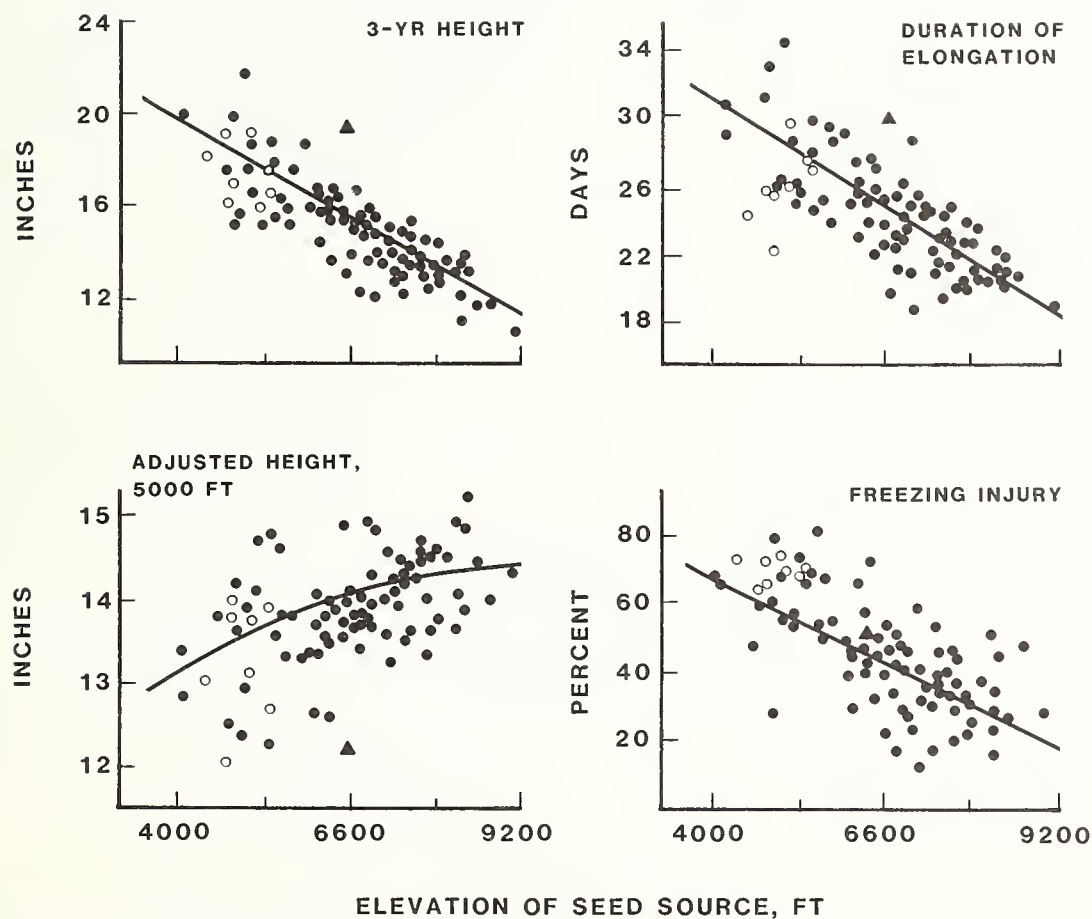


Figure 3.—Population means for four variables plotted by elevation of the seed source: • = lower Snake River Basin; O = Cascade Mountains; ▲ = Deadline Ridge.

The geographic model (table 5) was statistically significant for all variables except late growth, initiation of shoot elongation, and freezing injury. This model, however, accounted for less than a quarter of the variance in dependent variables that was not explained by elevation. Thus, the geographic model accounted for less than 10 percent of the total variance among populations. Consequently, elevational clines tend to be steep, but geographic clines tend to be gentle. Geographic variables plus elevation (the combined model) accounted for 28 to 74 percent of the variance among populations.

Geographic patterns of genetic variation that are independent of elevation are presented in figure 4 for several traits. These patterns were generated from values predicted from the geographic model. The contour interval is scaled to a value equaling half the least significant difference (Steel and Torrie 1960) among populations at the 80 percent level of probability [$\frac{1}{2} lsd(0.2)$]. Because values of *lsd* were calculated from the analysis of variance (table 2), contours represent about half the geographical distance associated with population

differentiation at the 80 percent level of probability. Contouring was begun with the overall mean, the zero deviation from the elevational regression.

All variables for which the geographic model was significant presented similar patterns of genetic variation. Those variables selected for figure 4 illustrate patterns of greatest divergence. In general, populations from the Salmon River drainage in the northeast portion of the region are of highest growth potential and least hardiness. Clines of decreasing growth potential and increasing hardiness radiate to the south and west. Only leaf length presents a divergent pattern: leaf lengths decline from west to east. Similar elevational and geographic clines result from significant intercorrelations among variables (table 6). Particularly noteworthy are the correlations among variables associated with growth potential. Whether measured in the field or greenhouse, these correlations were particularly strong ($r > 0.75$).

Regression analyses also clarify the interaction of populations and test environments for adjusted height (table 2). Elevational models showed that population

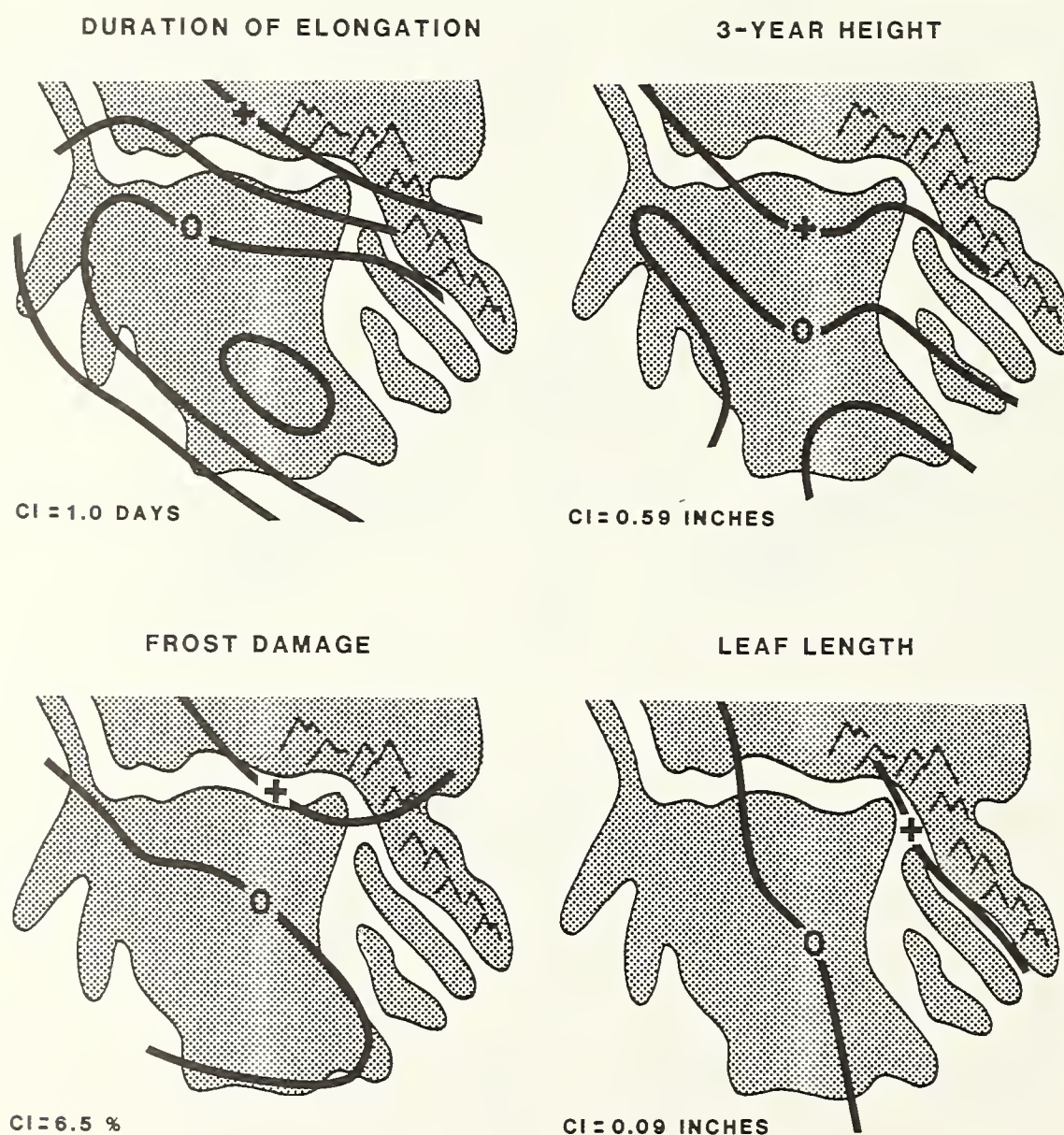


Figure 4.—Geographic patterns of variation that are independent of elevation. Shading marks the distribution of lodgepole pine in relation to the Bitterroot Range. C.I. = the contour interval, which is scaled to a value of $\frac{1}{2} lsd(0.2)$. The zero contour represents the mean of all populations standardized for elevation.

Table 6.—Correlation matrix relating population means for all studies¹

Variable	Code	LL	H	AH1	AH2	FI	I	D	R	C	EL	IN
Growth and development												
Late growth	LG	0.53	0.39	0.40	−0.17	0.12	0.04	0.39	0.31	0.39	0.40	0.30
Leaf length	LL		.61	.57	−.26	.43	.04	.61	.57	.62	.64	.47
Height	H			.76	−.49	.60	.05	.87	.77	.88	.89	.26
Adjusted height (2,200 ft)	AH1				−.12	.54	.10	.73	.53	.74	.72	.52
Adjusted height (5,000 ft)	AH2					−.16	−.01	−.46	−.30	−.46	−.42	−.33
Frost injury	FI						−.10	.54	.51	.53	.57	.41
Periodicity of shoot elongation												
Initiation	I							−.04	−.24	.03	−.11	.30
Duration	D								.77	.99	.95	.54
Rate	R									.76	.91	.38
Cessation	C										.94	.56
Elongation	EL											.52
Cold hardiness												
Injury	IN											

¹Coefficients of absolute value >0.22 are statistically significant at the 5 percent level.

means for adjusted height measured at high elevation were positively correlated with elevation of the seed source (fig. 3). But when measured at low elevations, population means were negatively associated with the elevation of the seed source. Thus, between years 2 and 3, trees from high elevations were beginning to perform the best at the high elevation site, while trees from relatively mild environments at low elevation were expressing the best performance on the site at low elevation.

The performance of populations from geographic regions peripheral to the region of study is presented in

table 7 relative to that expected for populations in central Idaho from similar elevations. Populations from the Cascades of central Oregon expressed both a lesser growth potential and lesser hardiness than populations from central Idaho. These differences are particularly emphasized in studies of shoot elongation. Populations from the Cascades started elongation late, ceased early, and grew at a slow rate. In contrast to the comparative performance of Cascade populations, the disjunct southern population from Deadline Ridge expressed a growth potential that exceeded that of populations at similar elevations in central Idaho.

Table 7.—Average difference between the observed performance of peripheral populations and that expected from the elevational regression for populations from central Idaho

Variable		Cascade Range	Deadline Ridge
Growth and development			
Late growth	(inches)	−0.00	0.08
Leaf length	(inches)	−.28	.29
Height	(inches)	−.46	4.34
Adjusted height (2,200 ft)	(inches)	.19	1.48
Adjusted height (5,000 ft)	(inches)	−.28	−4.35
Frost injury	(percent)	−2.00	9.10
Periodicity of shoot elongation			
Initiation	(days)	.90	.10
Duration	(days)	−2.30	5.40
Rate	(in/day)	−.00	+ .00
Cessation	(days)	−.06	.20
Elongation	(inches)	−.48	.90
Cold hardiness			
Injury	(percent)	10.20	1.90

DISCUSSION

Genetic differentiation among populations from the lower Snake River Basin, like that for populations from northern Idaho (Rehfeldt 1983), Utah (Rehfeldt 1985a) and Oregon (Stoneman 1985), occurs along relatively steep clines. Differentiation was detected for a variety of traits, most of which were intercorrelated. Strong intercorrelations among adaptive traits result from either or both genetic linkage and parallel selection. Regardless, coherence (Clausen and Hiesey 1960) describes the system of genetic variability for a species such as lodgepole pine that is physiologically specialized for specific environments. Populations from mild environments are of high growth potential and low hardiness. Populations from severe environments are of high hardiness and low growth potential. Adaptation in lodgepole pine can be viewed as a balance between selection for high growth potential in mild environments and selection for high cold hardiness in severe environments.

Because adaptive clines parallel environmental gradients, it is not surprising that elevational clines are pronounced. Temperatures and, consequently, the length of the growing season decrease as elevation increases. Regression coefficients indicated that populations separated by 3,000 feet are expected to differ, for example, by 35 percent in 3-year height, 25 percent in injury from spring and fall freezing, and 0.3 inch in leaf length.

Geographic patterns of genetic variation also tend to correspond to environmental gradients, particularly those gradients reflected by the frost-free period (fig. 5). The influence of the Salmon River drainage on both climatic and genetic gradients (figs. 4 and 5) is particularly striking. The northeast portion of this drainage is not only characterized by a relatively mild climate, but also presents to the distribution of lodgepole pine the largest acreage of relatively mild climate in central Idaho. Consequently, it is the performance of populations from the northeast that drives the geographic regression. These populations are of highest growth potential and least hardiness. Toward the south and southwest, however,

the mild climate deteriorates rapidly. Populations correspondingly express declining growth potential and increasing hardiness.

Elevational clines are much steeper than the geographic. A comparison of these clines is possible from figure 4 in which each geographic band, situated between any two contours, is standardized for elevation. Each band is equivalent to the amount of genetic variation that occurs across 345 feet, 425 feet, 1,050 feet, and 1,150 feet of elevation for 3-year height, duration of elongation, frost injury, and leaf length, respectively. Thus, in a region that spans 150 miles from north to south, geographic clines for those variables in which population differentiation was pronounced (table 5) are equivalent to an elevational cline of about 1,000 feet at a single locality.

Patterns of adaptive variation have direct implications in forest management. To limit maladaptation in planted trees, seed transfer guidelines must reflect adaptation. One estimate of an appropriate limit to seed transfer involves the smallest geographic or elevational interval across which differentiation can be detected (Rehfeldt 1979). This interval is estimated by the ratio $lsd(0.2)/b$, where b is the regression coefficient and $lsd(0.2)$ is derived from the analysis of variance as the least significant difference among population means at the 80 percent level of probability. (A rather low level of probability is used to avoid accepting no differences when differences actually exist.)

Elevational intervals associated with $lsd(0.2)$ included 680 feet for 3-year height, 890 feet for the duration of shoot elongation, 1,560 feet for freezing injury, 2,300 feet for leaf length, and 3,440 feet for late growth. These intervals suggest that the maximum elevational limits for biologically sound seed zones should not be much greater than 700 feet. This means that the transfer of seed from a single source should be limited to ± 350 feet. Nevertheless, considerable genetic differentiation is expected across seed zones that are only 700 feet thick. These differences, for instance, amount to about 8 percent in 3-year height and nearly 6 percent in susceptibility to cold injury.

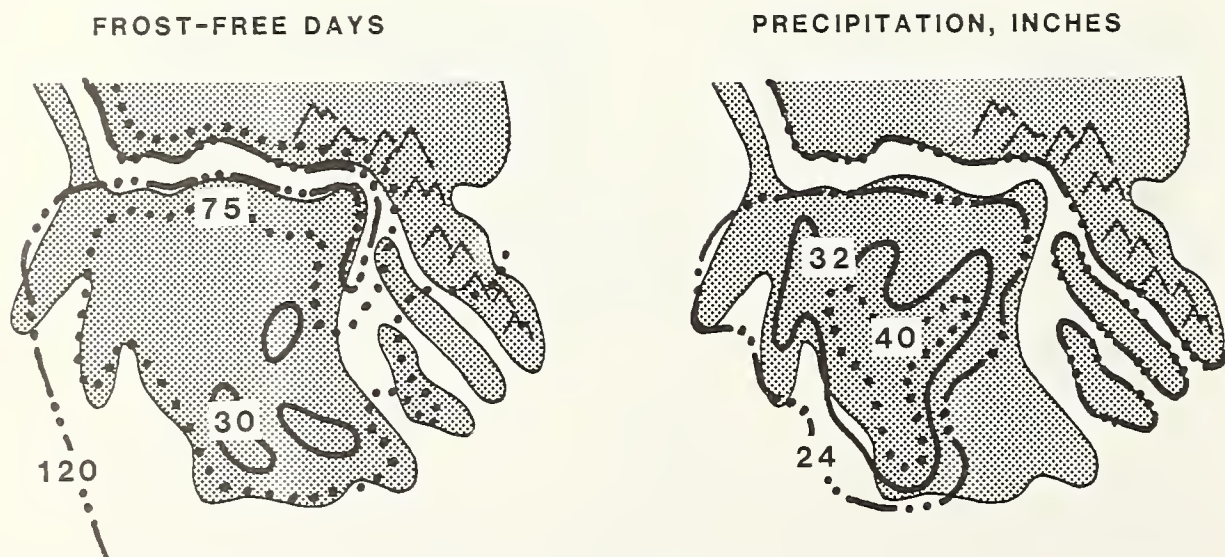


Figure 5.—Geographic patterns in precipitation and frost-free period for the lower Snake River Basin (from U.S. Department of Commerce 1968).

Geographic patterns of variation (fig. 4) were scaled to a value of $\frac{1}{2}lsd(0.2)$, and therefore, lateral transfers of seed should be limited to about ± 1 contour. This means that two geographic zones are sufficient for lodgepole pine in the lower Snake River drainage.

The appropriate size of seed zones should be practical administratively and economically. Thus, limits to seed transfer must accommodate biology and economics, while being operationally feasible. When, however, feasibility and economics demand an alteration in the guidelines proposed above, it should be remembered that each geographic band of figure 4 is equivalent genetically to a relatively small elevational interval within a locality. Consequently, the geographic limits should be compromised. From the biological viewpoint, seed zones for the lower Snake River Basin should be considered as elevational zones with geographic stratification.

Regardless, populations of lodgepole pine from the lower Snake River display patterns of genetic variation that seem to typify the adaptation of the species to heterogeneous environments in other geographic localities. Populations appear to be physiologically attuned to specific environments, clines are steep, and genetic differences occur across relatively small environmental intervals. Differentiation among populations is easy to detect experimentally and is closely related to geography and elevation of the seed origin. Therefore, seed transfer in artificial reforestation should be limited greatly.

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Genetic differentiation of 89 populations of *Pinus contorta* primarily from central Idaho was studied in field, greenhouse, and laboratory tests. Analyses of variables reflecting growth potential, morphology, cold hardiness, and periodicity of shoot elongation revealed population differentiation for a variety of traits. Regression models related as much as 77 percent of the variance among population means to the elevation and geographic location of the seed source. For genetic variation to be arranged along relatively steep environmental clines implies pronounced adaptive differentiation. As a result, seed transfer in reforestation should be restricted severely if maladaptation is to be controlled.

KEYWORDS: microevolution, adaptation, population differentiation, seed zones, seed transfer
